

Genetic analysis of coevolution between plants and their natural enemies

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Plants exhibit a diverse array of characteristics that have been interpreted as functioning primarily as defenses against natural enemies, such as pathogens and herbivores. Recent genetic analyses of resistance provide evidence supporting this interpretation. In addition, these analyses also support a key assumption underlying models of the evolution of resistance (i.e. that resistance is costly) and suggest that the outcome of coevolution is often not explainable in terms of pairwise interactions between a plant and individual natural enemies (i.e. coevolution is often likely to be diffuse rather than pairwise).

The selective impact of natural enemies

Numerous ecological manipulations involving the experimental removal of natural enemies have demonstrated that attack by pathogens and by herbivores generally decreases plant survival, growth rate or reproductive success^{17,18}, as does the addition of natural enemies, as is often seen in biological control programs. Although this type of evidence is often interpreted to indicate that natural enemies impose strong selection on their hosts, these studies uniformly fail to determine whether enemy impact differs among plant genotypes. Because natural selection is, by definition, differential fitness among genotypes, these studies do not provide any indication of the magnitude of selection, if any, that natural enemies impose. At best, they indicate the potential for selection, that is, an upper bound on the magnitude of selection.

Rigorous demonstration that natural enemies impose selection on their host plants requires a research protocol consisting of three sequential steps. (1) The character on which natural selection is suspected to act must be shown to be genetically variable. In general, most suspected 'defensive' characters, as well as general susceptibility to damage or infection, have been found to exhibit some degree of genetic variation^{3,19}.

(2) The character should be demonstrably subject to some form of selection. In general, selection on a character is typically measured in either of two ways: by phenotypic correlations between the character and fitness^{20,21} or by demonstrating that genotypes affecting the character differ in fitness. Of these methods, the latter is preferred because phenotypic measures of selection can be biased by environmentally induced correlations between characters and fitness^{22,23}. Such environmental correlations are likely to be common for resistance characters, especially secondary chemicals, the concentrations of which have been shown frequently to be influenced by soil nutrient and water content²⁴. Recent assessments using a genetic criterion

It has been estimated that terrestrial plants and their natural enemies (including viral, bacterial and fungal pathogens, and invertebrate and vertebrate herbivores) constitute approximately half of the species of extant organisms¹. Moreover, plants exhibit a tremendous diversity of apparently defensive characteristics, including trichomes (hairs) and spines, secondary chemical compounds, temporal avoidance of enemies and structures that attract enemies of their natural enemies^{2,3}. At the same time, the natural enemies of plants exhibit a bewildering array of behavioral, morphological and physiological characteristics that facilitate exploitation of their host plants and circumvention of these apparently defensive characters^{4,5}. Accounting for the generation of this diversity has been a major preoccupation of evolutionary biologists for nearly a century.

Although antecedents can be traced back to early work by Stahl⁶, Brues⁷, Dethier⁸ and Fraenkel⁹, the hypothesis that much of this diversity has arisen as a product of coevolution between plants and their natural enemies was crystallized by Ehrlich and Raven¹⁰. Since this seminal paper, it has been recognized that 'coevolution' actually refers to a set of processes that differ in details, such as the number of interacting species, the taxonomic relationships between the interacting species and the persistence of the interactions^{11,12}. Nevertheless, all of these processes have two features in common: (1) selection imposed by natural enemies causes plant populations to diverge in 'defensive' characteristics; and (2) selection imposed by plant 'defensive' characteristics causes natural enemy populations to diverge in characteristics associated with exploitation of the host plant. During this period, a great deal of effort has been directed towards documenting the operation of coevolution, and towards understanding the kinds of evolutionary and ecological patterns that coevolution is expected to generate. It can be safely said, based on the evidence that has accumulated, that there is little disagreement among biologists that assertion (2) is generally valid¹³. More controversial, however, is the notion that selection imposed by natural enemies, and particularly by herbivores, has generated a significant proportion of the biochemical and structural diversity exhibited by plants. In particular, many workers have argued that selection by natural enemies is normally too weak to account for the evolution of traits such as secondary compounds, and that other evidence suggests that these kinds of characters perform other useful ecological functions¹⁴⁻¹⁶.

One reason for the persistence of this controversy is that historically there has been little way to distinguish between these views empirically. However, recent genetic analyses of interactions between plants and their natural enemies are providing evidence that plant-enemy coevolution is common in natural communities. Moreover, these analyses reveal important information about constraints on coevolutionary processes in the form of costs of resistance and diffuse (non-pairwise) interactions among coevolving species. The purpose of this review is to describe how a genetic approach has led to these new insights about the nature of coevolution and its contribution to biotic diversity.

for selection frequently indicate that putative defensive characters, such as trichomes and secondary compounds, are subject to selection under field conditions (Refs 25–29; D.H. Siemens and T. Mitchell-Olds, unpublished).

(3) The manipulation of natural enemy abundance (e.g. reduction or elimination by spraying with pesticides or caging out herbivores) should be undertaken to determine whether the pattern of selection acting on the character changes depending on whether natural enemies are present or absent, that is, whether natural enemies contribute to selection on the character. Failure to manipulate the presence or absence of natural enemies can lead to improper inferences regarding the nature of selection on variation for resistance (as measured in the second step above) in at least two ways. In the first case, selection that appears to be due to enemies might be due to selection by other ecological factors on either pleiotropic manifestations of resistance genes or on genes in linkage disequilibrium with resistance genes³⁰. In the second case, observation of selection favoring reduced resistance under natural conditions²⁶ could be interpreted as indicating the absence of positive selection by natural enemies when such selection exists, but is not of sufficient magnitude to overcome the costs. In both of these cases, decoupling the component of selection imposed by natural enemies from that imposed by other factors is necessary, and can be achieved only by experimental manipulation of the presence of natural enemies.

Three studies carrying out all three steps of this protocol provide evidence that natural enemies impose selection on resistance characters in natural populations of their host plants. Simms and Rausher³¹ demonstrated that elimination of herbivores from the morning glory *Ipomoea purpurea* also eliminates additive genetic variation for fitness, as measured by total seed production over the lifetime of a plant. Moreover, they demonstrated that resistance to capsule-feeding herbivores is subject to selection when herbivores are present. Because there can be no selection on any character when there is no additive genetic variation for fitness, these results indicate that capsule-feeding herbivores impose selection on resistance to those herbivores, and, in fact, are responsible for all of the selection on variation for resistance. In a similar investigation, Biere and Antonovics³² report, but do not compare, the relationships between male fitness in *Silene alba* (white campion) in the presence and in the absence of the anther smut fungus, *Ustilago violacea*. Analysis of their data reveals that the presence of the smut alters the pattern of selection on fungal resistance in *S. alba* (Fig. 1). Interestingly, the detrimental impact of the smut is largest for genotypes with intermediate levels of resistance. This

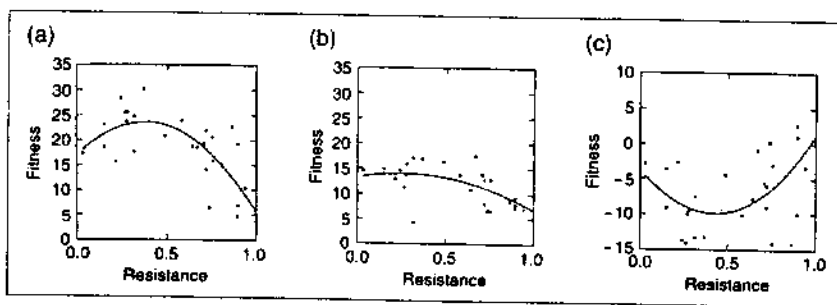


FIGURE 1. The relationship between mean male fitness and field resistance to the smut fungus *Ustilago violacea* in *Silene alba*. Each point represents estimated mean male fitness and mean resistance for a particular family in the experiment. Field resistance represents 1 minus the proportion of individual plants infected in field experiments in which plants were exposed to pathogens. Male fitness for an individual plant was estimated as a weighted average, over census days, of the number of male flowers produced by a plant divided by the total number of male flowers produced by all plants. (a) Plants not exposed to pathogens. The linear and quadratic terms of regression of fitness on resistance are both significant (degrees of freedom: 1, 24 in both cases; F -values: 15.92 and 9.56; P -values: <0.001 and 0.005 for linear and quadratic terms, respectively). (b) Plants exposed to pathogens. Linear term of regression is significant (degrees of freedom: 1, 24; F -value: 4.09; P -value: 0.055). (c) Regression of difference in fitness between plants exposed and not exposed to pathogens (y axis) on resistance. This curve represents the pattern of selection imposed by the pathogen. The linear and quadratic terms of regression are both significant (degrees of freedom: 1, 24 in both cases; F -values: 7.51 and 5.34; P -values: <0.015 and 0.03, respectively), indicating that the pattern of selection in the disease-free treatment differs in slope and in curvature from that in the diseased treatment. (Data used in this analysis were provided by Biere and Antonovics³².)

pattern arises because, in the absence of pathogens, an intermediate level of resistance is favored (Fig. 1a). One possible explanation for stabilizing selection of this sort is that while late flowering contributes greatly to resistance, it also directly causes a reduction in total number of flowers produced and, hence, a reduction in male success³². Finally, Mauricio (PhD thesis, Duke University, 1995) found that elimination of herbivores from experimental populations of *Arabidopsis thaliana* altered the pattern of selection on trichome density and total glucosinolate concentration, both of which reduce herbivore damage in the field. In the absence of herbivores, the fitness peak corresponded to genotypes with no trichomes or glucosinolates. Herbivores imposed selection that favored increased levels of glucosinolates and trichomes. In the case of glucosinolates, the strength of selection was sufficient to overcome the costs of these compounds, yielding stabilizing selection on glucosinolate levels. By contrast, for trichomes, the benefits did not exceed the costs, yielding net selection for the absence of trichomes even in the presence of herbivores.

Although it is dangerous to generalize from the results of three studies, the observation of natural-enemy-imposed selection in all three studies of this type suggests that natural enemies, including herbivores, can commonly guide the evolution of purportedly defensive characters in plants. In particular, these genetic investigations suggest that much of the potential for selection by natural enemies demonstrated by ecological studies is frequently realized. Nevertheless, some evidence indicates that, at least in some cases, 'defensive' characters are selected for even in the absence of natural enemies, indicating that these characters have ecological functions other than, or in addition to, protection of the plant from natural enemies^{27,32}.

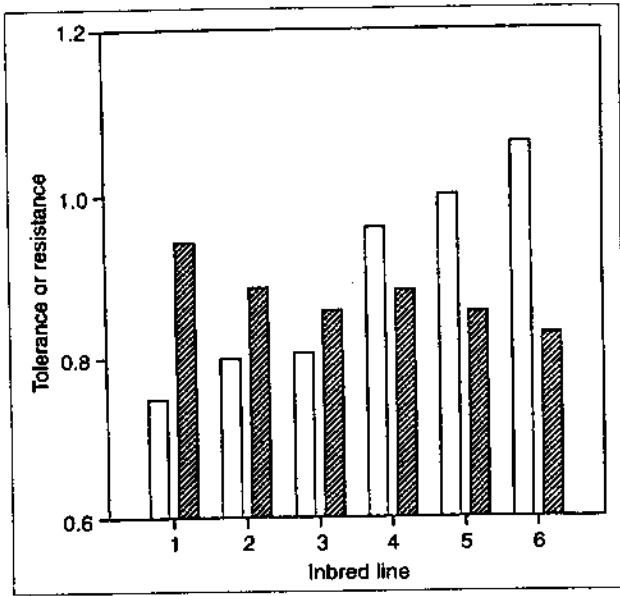


FIGURE 2. Trade-off between resistance (hatched bars) and tolerance (open bars) to apical meristem damage in *Ipomoea purpurea*. Resistance and tolerance were estimated for six inbred lines. Resistance was estimated in a field experiment as the proportion of plants of an inbred line that did not exhibit damage to the apical meristem. Tolerance for each inbred line was estimated in a greenhouse experiment as the ratio (number of seed capsules produced by damaged plants per number of seed capsules produced by undamaged plants), where damaged plants had the apical meristem removed approximately one month after germination. (Redrawn from Fineblum and Rausher⁴⁰.)

Costs of resistance

The frequent observation of genetic variation for resistance characters in natural populations, coupled with the almost universal detriment to plant fitness caused by attack from natural enemies, poses a dilemma: why does selection imposed by natural enemies not cause an evolutionary increase in levels of resistance? The traditional resolution of this dilemma has been to postulate that resistance is costly, that is, pleiotropic effects of alleles for resistance cause an incremental decrease in fitness, even though the direct effects of those alleles in reducing herbivory are beneficial. Models of selection on resistance that incorporate such costs demonstrate that, in general, trade-offs between costs and benefits of resistance can stabilize resistance at levels less than what is genetically achievable in a population³³⁻³⁵.

Recent analyses of genetic correlations between resistance traits and other characters have not only provided strong evidence that costs of resistance are common in natural populations, but have also revealed that there are several categories of costs. One type of cost, termed 'allocation cost', results because plant resources directed toward resistance characters are withheld from other characters that enhance survival, growth and reproduction. Such costs are typically revealed by demonstrating that, in an environment free of natural enemies, genotypes conferring high resistance have low fitness relative to genotypes conferring low resistance (Refs 20, 32, 36; R. Mauricio, PhD thesis, Duke University, 1995).

A second type of cost, termed 'ecological' cost, arises when genotypes resistant to one kind of natural enemy are susceptible to a second kind of natural enemy and vice versa. The natural history of interactions between plants and their enemies has suggested that this kind of cost is likely to be frequent in nature³⁷. For example, cases are known in crop plants in which a gene conferring resistance to one herbivore renders a plant more susceptible to other herbivores³⁸, and many cases are known in which particular plant secondary compounds are toxic to some herbivores but attract other herbivores. Nevertheless, it is only recently that definitive evidence for such trade-offs, in the form of negative genetic correlations between resistance to different enemies under field conditions, has been obtained for natural plant populations (Ref. 39; D.H. Siemans and T. Mitchell-Olds, unpublished).

A final type of cost, which was recently discovered, is a trade-off between resistance and tolerance to the same natural enemies. While tolerance can be viewed as a type of defense against natural enemies, it differs from resistance in that resistance is the average amount of damage experienced by a genotype for a given abundance of natural enemies, whereas tolerance is the average amount by which the fitness of a genotype is reduced for a given amount of damage. Fineblum and Rausher⁴⁰ showed that genotypes that were resistant to herbivores that damage the apical meristem of *I. purpurea* were less tolerant of damage by those herbivores, and vice versa (Fig. 2). In one sense, this type of trade-off between resistance and tolerance could be viewed as an allocational cost, because presumably it results from the diversion of resources away from unknown characters that are responsible for tolerance. Nevertheless, this type of cost differs from a true allocation cost, in that allocation costs are manifested in the absence of natural enemies, while a cost of resistance in the form of reduced tolerance is not. Because several investigations have failed to detect this type of 'tolerance' cost to resistance (Ref. 28; R. Mauricio, PhD thesis, Duke University, 1995), it is clear that such costs are not universal, but there is little indication, currently, of how common they might be in natural plant populations.

The distinction between types of resistance cost is of interest primarily because different types of cost can constrain the evolution of resistance in different ways. For example, a theoretical comparison of allocation and tolerance costs indicates that with allocation costs, selection on resistance is always stabilizing or directional, while with tolerance costs selection can also be disruptive⁴⁰. Another potential difference involves evolutionary amelioration of costs by selection at modifier loci^{37,41}. Intuitively, it seems plausible that amelioration of ecological costs might be easier than amelioration of allocation or tolerance costs because amelioration of ecological costs might be accomplished by altering, say, a plant secondary compound (e.g. by methylation or hydroxylation) in order to render it less attractive to adapted natural enemies, while not changing its toxicity to non-adapted enemies. By contrast, ameliorating allocation or tolerance costs might often involve either the reorganization of a biochemical network or reducing the effectiveness of resistance³⁷. Despite these considerations, the theoretical implications of different types of resistance costs are largely unexplored.

Whether costs are due to pleiotropy or linkage disequilibrium is a central issue in understanding the evolution of resistance. In outbreeding species, linkage disequilibrium is expected to decay unless a particular pattern of selection is actively maintaining it. Consequently, linkage disequilibrium serves only as a temporary constraint on the evolution of resistance. Even when maintained by selection, it will probably not constrain the evolution of resistance in novel directions, because a change in the pattern of selection that pushes resistance in a different direction is likely to destroy the very pattern of selection that maintains the linkage disequilibrium. Thus, it is generally assumed that only costs owing to pleiotropy can constrain the evolution of resistance for significant periods of time³⁶.

Although accumulating evidence for allocation costs of resistance is strong, whether or not apparent pleiotropic effects of resistance reflects true pleiotropy of resistance genes, or is due, instead, to the effects of nonresistance genes that are in linkage disequilibrium with resistance genes, has not been resolved. It is expected that in outcrossing natural populations there has been sufficient time for recombination to break up such linkage disequilibrium, even for very tightly linked genes³⁶. Finding the same pattern of costs in several different populations is, therefore, likely to reflect true pleiotropy (R. Mauricio, PhD thesis, Duke University, 1995). However, it is becoming clear that recombination rates can be highly variable across the genome⁴², leading to the expectation that linkage disequilibrium should be common in regions of low recombination⁴³. These observations suggest that apparent pleiotropy of resistance genes could be caused by tightly linked nonresistance genes, especially if the resistance genes are located in regions of low recombination. In this case, similar patterns of costs across populations could simply reflect the geographic spread of linkage disequilibrium. This effect is likely to be even more pronounced in species that are mainly selfing or apomictic, in which linkage disequilibrium is expected to develop even between unlinked genes⁴⁴.

The issue of pleiotropy versus linkage disequilibrium cannot be resolved until the physiological and molecular bases of resistance costs are understood, because this will require the identification of the gene(s) responsible for those costs. Nevertheless, this distinction might be moot if linkage disequilibrium is so tight and stable (owing to very low recombination) that resistance, and its apparent costs, are inherited together as a unit. In this case, costs will constrain the evolution of resistance in a way that is indistinguishable from what would be observed if they reflected true pleiotropy.

Pairwise versus diffuse selection

Two major classes of coevolution between plants and their natural enemies have been recognized: pairwise and diffuse^{11,12}. Because the conceptual distinction between these two classes has been somewhat clouded^{45,46}, little empirical evidence exists to indicate which of these two classes is more prevalent in nature. Recently, however, straightforward definitions of these processes have been proposed: pairwise coevolution between a plant and two enemies occurs if the trajectory of coevolution between the plant and one of its

enemies does not depend on whether the other enemy is present⁴⁷; otherwise, coevolution is diffuse. This definition is readily extended to multiple enemies and multiple hosts, and leads naturally to a twofold criterion for the operation of diffuse coevolution⁵⁶. This criterion is expressed here in terms of the pattern of selection exerted on a host plant by two species of enemy, although, in principle, it can also be expressed in terms of selection exerted by the plant on its natural enemies. Selection and the response to selection are pairwise if (1) resistance to one enemy is genetically uncorrelated with resistance to the other, and (2) the pattern of selection imposed by one enemy is independent of whether the other enemy is present or not; otherwise, selection is diffuse. These criteria flow naturally from the general multivariate equation for evolution of quantitative characters⁴⁸ (Box 1).

Recent investigations that have examined the pattern of genetic correlations among resistances to different natural enemies in natural plant populations reveal an interesting pattern: despite expectation, negative correlations among resistances are relatively uncommon. There seems to be little evidence to suggest that genetic constraints arising from ecological costs commonly retard the evolution of resistance. Instead, resistances tend to exhibit either no genetic correlations or positive correlations (Table 1). In many systems, then, resistances to different enemies are controlled by different sets of genes [criterion (1) is satisfied], and are, therefore, free to evolve independently if the patterns of selection exerted by different enemies are independent.

While current evidence suggests that criterion (1) for pairwise coevolution can frequently be satisfied, the same cannot be said for criterion (2). Of five studies that have explicitly sought to determine whether the presence of one enemy alters the pattern of selection imposed by others, four have obtained evidence suggesting such an effect^{29,47,49-51}. In *Rhus glabra* (smooth sumac), for example, feeding by chrysomelid beetles reduces the negative impact of deer on fitness, thus reducing the potential for deer to exert selection⁴⁹. In natural populations of birds rape (*Brassica rapa*), independent experimental manipulation of the abundances of two herbivores, flea beetles (*Phyllotreta cruciferae*) and diamondback moths (*Plutella xylostella*), indicated that when damage by moths was low, increasing levels of damage by flea beetles resulted in reduced plant fitness, whereas when moth damage was high, increasing levels of damage actually increased plant fitness (Fig. 3)⁵⁰. Both of these examples indicate that the detrimental impact of one herbivore species and, hence, the potential for selection exerted by that species, depends on the presence of the other species. In the goldenrod *Solidago altissima*, genetic variation for susceptibility to the aphid *Uroleucon tissoti* is actually caused by variation in susceptibility to those insect herbivores that damage the apical meristem and cause the plant to branch. Genotypes with high susceptibility to these insects experience increased branching. Increased branching, in turn, increases the number of aphids attacking a plant⁵¹. Although the selective impact of aphids has not been quantified in this system, aphids frequently decrease plant fitness significantly⁵². These results imply that any selection imposed by *Uroleucon*

Box 1. Lande's equation and the criteria for pairwise coevolution

The basis for criteria (1) and (2) for pairwise coevolution can be understood by examining Lande's⁴⁸ general equation for multivariate evolution of quantitative characters, here expressed in terms of overall resistance to two natural enemies, z_1 and z_2 :

$$\Delta \bar{z} = G P^{-1} s = G \beta \tag{1}$$

Or, in expanded form:

$$\begin{bmatrix} \Delta \bar{z}_1 \\ \Delta \bar{z}_2 \end{bmatrix} = \begin{bmatrix} G_{11} & G_{12} \\ G_{12} & G_{22} \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} = \begin{bmatrix} G_{11}\beta_1 + G_{12}\beta_2 \\ G_{12}\beta_1 + G_{22}\beta_2 \end{bmatrix} \tag{2}$$

In this equation, $\Delta \bar{z} = [\Delta \bar{z}_1, \Delta \bar{z}_2]^T$ is the vector describing the change in mean level of resistance to each enemy; G and P are the additive genetic and phenotypic variance-covariance matrices for the resistances respectively; $s = [s_1, s_2]^T$ is the vector of selection differentials acting on resistance to each enemy; and $\beta = [\beta_1, \beta_2]^T$ is the selection gradient vector acting on the resistances. Although β is typically estimated using phenotypic regressions of fitness on resistance, genetic regressions (i.e. additive genetic value of fitness on additive genetic values of the characters) are more desirable because they avoid effects of environmentally induced covariances between fitness and resistance^{22,23}.

Inspection of this equation reveals that in order for z_1 to evolve independently of z_2 , G_{12} , the additive genetic covariance for resistances to the two enemies, must be zero [criterion (1) above], because if this is not the case, selection imposed by enemy 2 contributes to the change in z_1 [via the term $G_{12}\beta_2$ in Equation (2)]. A situation of particular interest is when resistances are negatively correlated (i.e. $G_{12} < 0$). Then, when enemy 2 is present, it retards, or even prevents, the evolution of increased resistance to enemy 1 (because $G_{12}\beta_2 < 0$), that is, coevolution is diffuse. By contrast, when resistances are positively correlated ($G_{12} > 0$), the magnitude of the response to selection by enemy 1 is increased by the presence of enemy 2 ($G_{12}\beta_2 > 0$), and is also technically diffuse. However, this type of constraint will not prevent or slow the evolution of resistance to either enemy and, thus, is less interesting.

Criterion (2) derives from the observation that even if the additive covariance for resistance is zero, change in z_1 might depend on whether enemy 2 is present or absent in a more subtle way: β_1 , the magnitude of selection acting directly on resistance to enemy 1, might depend on whether enemy 2 is present (or, more generally, on the value of β_2)^{47,49}. This dependence could arise either because the presence of enemy 2 alters the abundance of and, hence, the amount of damage caused by enemy 1, or because the presence of enemy 2 alters the impact of damage by enemy 1 on plant fitness⁴⁷.

on *Solidago* is conditional on the presence of insects that induce branching. Finally, in *I. purpurea*, the selective surface estimated from family means exhibits two peaks, one corresponding to resistance to the anthracnose *Colletotrichum dematium*, the other corresponding to resistance to tortoise beetles. Because in the absence of anthracnose the peak for resistance presumably disappears, selection will always favor the evolution of resistance to tortoise beetles. By contrast, if anthracnose is present and a population of *Ipomoea* evolves resistance to this pathogen, then subsequent selection will favor elimination of resistance to tortoise beetles. Thus, it appears that the presence or absence of anthracnose can influence the pattern of selection exerted by tortoise beetles and, therefore, whether resistance to tortoise beetles will evolve, and vice versa²⁹. Interestingly, this type of constraint arises despite a positive genetic correlation between resistances to the two types of natural enemies.

TABLE 1. Numbers of negative, positive and zero pairwise genetic correlations for resistance to natural enemies in several plant species

Plant species	No. of natural enemies	Sign of correlation			Ref.
		-	0	+	
<i>Solidago altissima</i>	17	9	100	27	40
<i>Ipomoea purpurea</i>	4	0	6	0	31
	5	0	4	1	29
	3	0	2	0	41
<i>Salix lasiolepis</i>	4	0	3	3	53
<i>Salix sericea</i>	3	1	1	1	54
<i>Brassica rapa</i>	3	0	2	1	55
	2	1	0	0	25

Conclusions

In summary, evidence from recent genetic experiments suggests several generalizations about the process of coevolution between plants and their natural enemies. First, and perhaps most importantly, is the observation that genetic variation for resistance is commonly subject to selection by natural enemies. Because the systems that provide this evidence are not obviously unusual in any way, this evidence suggests that natural enemies are likely to have been, and to continue to be, important selective agents guiding the evolution of plant characteristics, such as secondary compounds and morphological structures. In other words, these observations support the importance of 'co' in 'coevolution'. Second, evidence is accumulating to indicate that one of the key assumptions of models of the evolution of resistance - that resistance has costs - is often, though not necessarily universally, valid. These results suggest that an interesting question facing biologists is understanding the circumstances in which costs will or will not arise. The additional observation that costs come in a variety of types provides evolutionary biologists with the challenge of determining the extent to which different types of costs have different implications for the evolution of resistance characters. Third, although the number of cases is still limited, an emerging pattern is that coevolution, when it occurs, is likely to be diffuse rather than pairwise. Surprisingly, diffuse coevolution appears to arise not so much because resistances to different natural enemies are negatively correlated, but usually because the presence of some natural enemies alters the pattern of selection exerted by others on resistance.

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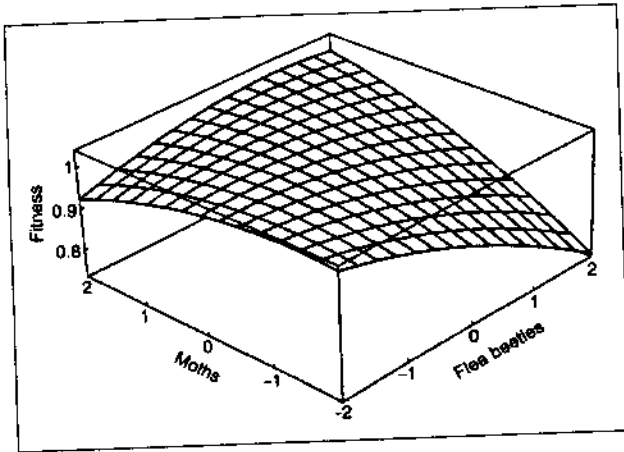


FIGURE 3. Relative fitness of *Brassica rapa* as a function of damage by two different natural enemies: diamondback moths (*Plutella xylostella*) and flea beetles (*Phyllotreta cruciferae*). Horizontal axes represent deviations, in units of standard deviation, from the mean amount of damage in the experiment. On the front edge, corresponding to moth damage held at a constant value of -2 standard deviation units, increasing amount of flea beetle damage has a substantial detrimental effect on plant fitness, whereas on the rear edge, corresponding to moth damage held at a constant value of +2 standard deviation units, plant fitness actually increases slightly with increasing flea beetle damage. Thus, the effect of flea beetles on plant fitness depends on the amount of moth damage experienced. (Redrawn from Pilson⁵⁰.)

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